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BIOLOGY OF *ANDRENA* (*SCRAPTEROPSIS*) *FENNINGERI* VIERECK (HYMENOPTERA: ANDRENIDAE), HARBINGER OF SPRING

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Abstract.—Andrena fenningeri Viereck is the first native bee species to fly each spring at Beltsville, MD; males appear as early as February 9, sometimes before their floral hosts begin to bloom. A permanent aggregation of nests in red clay was studied for 10 years. These univoltine, solitary bees break diapause and move at 4°C from their natal cells toward the soil surface in midwinter, ready to emerge and mate as soon as the topmost soil warms. They thermoregulate by aggregating their nests in the warmest available microclimate, and by basking on cold, sunny days to achieve the minimum 11°C required for flight. The most important host is *Acer rubrum*; *Prunus, Pyrus,* and *Salix* are also visited. Male swarming behavior, phenology, nest structure, and associates (including 5 *Nomada* spp., *Myopa* sp., and the behavior of 3 unusual species of *Eustalomyia* [Anthomyiidae]) are discussed. This bee may be manageable as an orchard pollinator, if suitable microhabitat and supplemental hosts are provided.

Key Words: bees, nests, thermoregulation, phenology, fruit pollination, *Eustalomyia,* conopids, *Acer*

The Holarctic bee genus *Andrena* includes about 700 Eurasian and 500 North American species; both species and individuals are dominant components of the bee fauna during springtime; they are important pollinators of crops and wild plants (see references in Batra 1990). The behavior and ecology of few species have been studied. Most species of *Andrena* are solitary, univoltine, polylectic bees; many of them share hosts, geographic ranges, and times of adult activity; the reasons why there are so many species of *Andrena* remain unknown.

This report concerns the nesting behavior of an Eastern, cold-adapted, polylectic, solitary species, which is the first native bee species to fly each spring at the Beltsville Agricultural Research Center (Prince George's Co., Maryland). Adult activity often begins while snow and ice remain on the frozen ground in shady places, and no plants are yet in bloom. *Andrena fenningeri* Viereck (det. W. E. LaBerge) is in the North American subgenus *Scrapteropsis,* which includes 18 vernal species (LaBerge 1971). The nesting behavior of only one of them, *A.* (*Scrapteropsis*) *alleghaniensis* Viereck, has previously been studied (Batra 1990). This solitary bee resembles *A. fenningeri* in its preference for *Acer* as a nectar and pollen source and in the location of its nest aggregation so as to maximize insolation.

I investigated the behavior of *A. fenningeri* at intervals over a period of 10 years (1987 to 1997), at an aggregation of nests in a sunny spot at the north edge of a large field (the "Rose Garden," off Entomology Rd.). Aggregations of nests of *Andrena* may persist for decades (Chambers 1968, Schönitzer and Klinksik 1990, 1992, Rid-

dick 1992). If the factors that permit or encourage permanent aggregations could be determined, this basic information may prove useful in conserving existing natural aggregations, and also for actively managing *Andrena* bees to pollinate fruit crops. For these reasons, the unusually early adult activity of *A. fenningeri* was investigated.

Materials and Methods

I made observations early in each season and during fair weather, when bees were flying. A total of 214 hours were spent, most of them during the unusually warm and early spring of 1990 (76 hours), and the cool, late spring of 1992 (60 hours). Entrances to nests with tumuli were marked with small, numbered aluminum tags, inserted 2 cm north of each nest. Meteorological data were recorded during visits. Soil temperatures at sites 1–6 were taken by inserting calibrated bimetallic dial probe thermometers to the appropriate depths. Nests were excavated by shovel and trowel after pouring plaster into them, which rendered tunnels easily visible. Adult bees and cleptoparasites were netted, then pinned, or preserved in FAA for dissection under a microscope. Pollen was stained with lactophenol-cotton blue and examined microscopically. I indicate means after ranges (in parentheses). Voucher specimens will be deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D. C.

Nests and their Contents

The nests of *A. fenningeri* in level ground (Fig. 1) were vertical tunnels that penetrated the uppermost humus-and-root-filled zone of the clay soil, to a zone of dense, poorly drained, red marine clay, where the cells were made. Nests ended at the top of a zone of gritty "hardpan." From late fall through early spring, the red clay was very moist, often muddy; after the tree canopy had leafed out in May (after adult bees ceased activity), the upper part of the clay dried to an adobe-like, hard consistency (soil penetrometer reading 3.5–4.5 kg/cm), providing protection to the growing brood and dormant adults in the cells. Evaporation and transpiration by plants during the hot and relatively dry summer months dried the clay. Rainy, cool weather, and the cessation of most transpiration after November permitted the soil to moisten and soften. Adult bees emerged from their cells in the softened soil, and crawled toward the surface of the soil during mid-winter. They waited just below the soil surface by late winter, ready to fly during the first warm days of spring.

A total of 22 entire nests was examined (5 in 1987; 3 in 1989; 14 in 1991). Because the lateral tunnels that led to cells were backfilled by the solitary mother bees with soil and obliterated after oviposition, many cells that were found could not be traced to their nests' tunnels (Fig. 1) The nests' tunnels reached depths of 16–25 (20.8) cm, and were 4.5–5.5 mm in diameter. Nest entrances were irregular, 3.5–5.5 mm in diameter, and when new, surrounded by a usually circular tumulus of loose, dry, soil particles 2.0–5.0 (3.3) cm in diameter and 0.5–1.0 cm high. The tumulus may not be rebuilt when it had disappeared due to rain. Nest entrances were often closed by loose soil particles when the bees were not foraging. The entrances to about 20% of the nests, which had been initiated beneath fallen leaves or in dense turf grasses, were difficult to find.

Nests had up to 5 brood cells (1.5) each. They were at the ends of lateral tunnels, which were 1.0–6.0 (2.5) cm long and 3.5–5.0 mm in diameter. Cells were made at depths of 13.0–26.0 (21.4) cm. The 39 cells were nearly horizontal, of the usual ovoid shape of *Andrena* cells, and coated internally with thin, shining, transparent waterproof linings, secreted by Dufour's glands. Cells were 10.0–12.5 (11.0) mm long, 5.0–6.0 (5.5) mm in maximum diameter, tapering to the cell's entrance, which was 2.5–4.0 (3.3) mm in diameter. After oviposition, this entrance was sealed with compressed

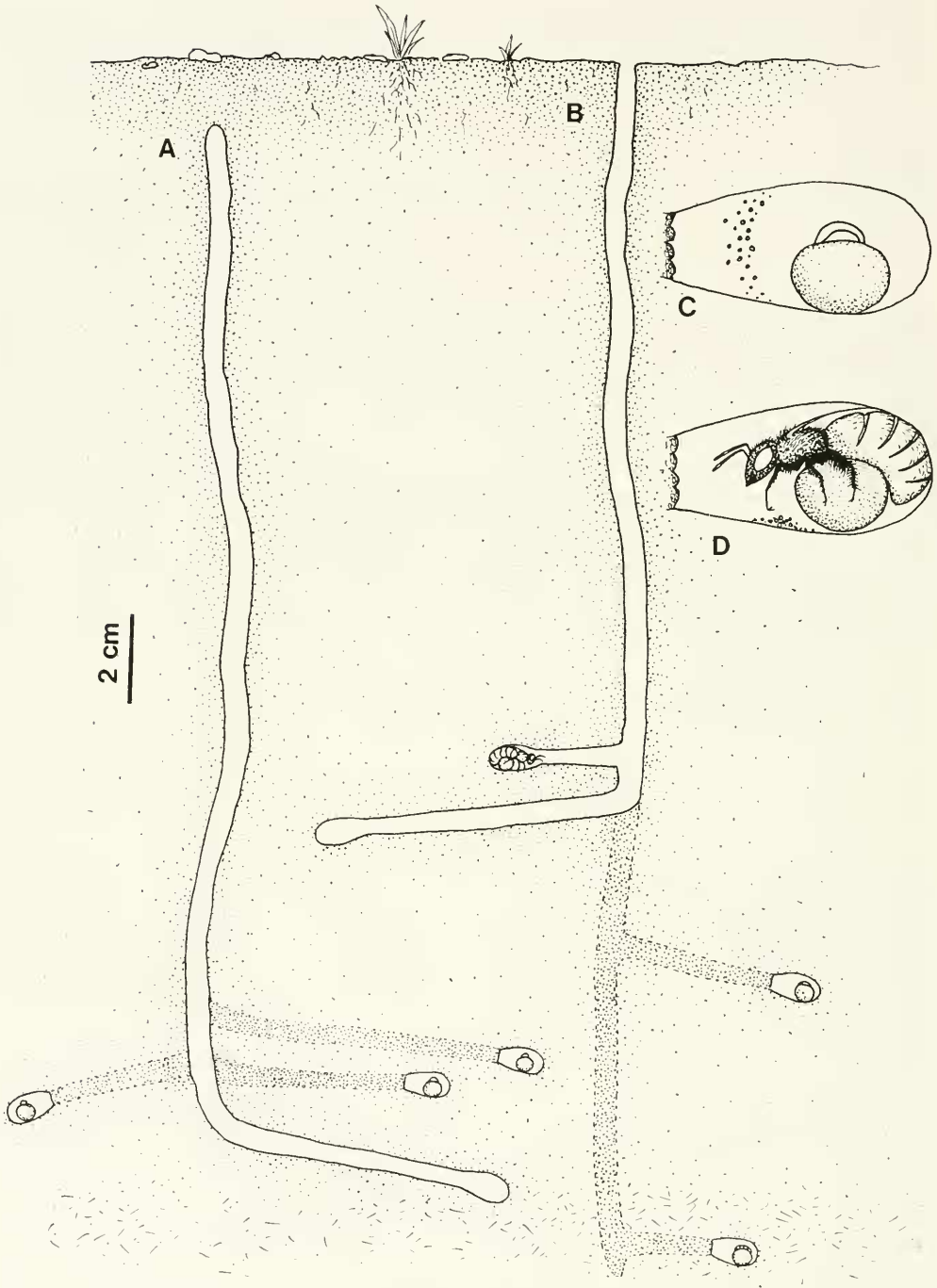

Fig. 1. Two nests of *A. fenningeri* in red marine clay soil(stippled area). Nests extended to a zone of denser soil (hardpan, hatched area), at a depth of 23 cm. The lateral tunnels that led to completed cells were filled with soil by the mother bees. Nest A, closed at the surface, was without an adult bee. It had 3 cells with eggs on pollen balls (examined May 4, 1989). Nest B was open, but without a tumulus. Two sealed cells contained eggs on pollen balls; one of these cells (C) had droplets of moisture on its thin, smooth waterproof lining. Another, open cell (D) had a dead female bee with a large, live conopid maggot filling her abdomen. She died in the position taken by bees when they oviposit (nest examined May 7, 1987).

soil pellets, laid down in two concentric rings around a central depression. The Dufour's-gland secretion in many genera of bees varies in composition. It polymerizes, forming a thin, smooth solid that waterproofs subterranean cells; it can also function as a pheromone, and as food for larvae. In *Andrena,* it is composed mainly of isoprenoid esters (see review in Ayasse et al. 1990).

Small, regularly-spaced, tasteless (to me) droplets, probably of water, were sometimes found on the hydrophobic cell linings, near the entrances of both empty and provisioned cells (Fig. 1C). Perhaps the shape of cells influences the condensation pattern, keeping water from condensing on the hygroscopic provisions, where it would permit spoilage. Yeasts in nectar and ambient fungi ferment and spoil the wetted provisions of many subterranean-nesting bees, causing significant mortality of their larvae (Batra 1970). The soil that seals entrances to cells and laterals of *A. fenningeri* is without a visibly water-repellent lining. It is porous, permitting some circulation of the water-saturated subsoil air. The survival of this bee, living inside cells for many months, and the preservation of its hygroscopic provisions inside humid cells, may depend on such a condensation-site-controlling feature of its brood cells.

Pollen balls (provisions) of *A. fenningeri* that had been made in early spring were olive-green, and composed solely of pollen of *Acer rubrum* L., mixed with nectar. Those made after *Acer* bloom were various shades of yellow, and made of up to 3 species of pollen. Pollen balls were firm, smooth, spheroid, somewhat flat on top, and 3.7–4.0 mm high and 4.0–4.8 mm wide (Fig. 1C). Occasionally, laterals and cells with large pollen balls, but no eggs or larvae, had been filled with earth. Eggs were strongly arched, white, 2.0–2.7 mm long and 0.5 mm thick. Larvae, ranging from 2.5–4.0 mm long, fed on top of the provisions; they later lay on their backs beneath their pollen balls, and reached 8 mm long when all their provisions had been eaten. Larvae transformed to prepupae in late May, after defecation. No cocoons were made. The times of pupation and transformation to adults were not studied.

The time of adult emergence each spring, foraging, oviposition, and larval development varied with weather conditions each year. Although individual females were not marked, many of their nests had been. The appearance of new tumuli late in spring where there had been no nests, the mid-season closure of nests that had been tagged in early spring, and the few cells per nest, indicated that some female *A. fenningeri* make more than one nest each, as do some other species of *Andrena.* At the end of the nesting season, during the first week of May, the old females became disoriented and exhibited displacement activity, such as random digging, as is seen in *Andrena nycthemera* Imhoff (Schönitzer and Klinksik 1990).

Floral Hosts

Andrena fenningeri is polylectic (La Berge 1971, Hurd 1979), visiting *Acer, Prunus, Pyrus, Salix,* and several other hosts. The first host to bloom each spring and the first to be visited for nectar and pollen at Beltsville was *Acer rubrum.* This is a dominant tree, occupying about 20% of the forest canopy near the nests. It is an important food resource for a wide variety of insects, available just as the insects emerge from hibernation (Batra 1985). The first provisions made by *A. fenningeri* were composed of the olive-green pollen from *A. rubrum.* In this respect, *A. fenningeri* resembles a related species, *A. (Scrapteropsis) alleghaniensis* Viereck, which provisions its cells with maple pollen in New York (Batra 1990). Several species of maple trees provide nectar and pollen for various other *Andrena* bees in Europe (Chambers 1968) and North America (LaBerge 1971; more references in Batra 1990). After the red maples finished blooming, *A. fenningeri* visited flowers of *Prunus, Pyrus*

and forbs, growing near the aggregation. Thus, the provisions that were made later in spring were yellow.

The time of emergence of adult *A. fenningeri* in some years coincided with the beginning of bloom of *A. rubrum* and *Salix* sp. In other years, the bees emerged a few days before any host plants had started to bloom. They mated, and began nesting, without having eaten anything. For example, 2 of 3 females that were starting to excavate nests on February 28, 1992, were inseminated, but all 3 had empty crops; 14 of 15 males in a mating swarm on that day had empty crops (one had eaten some maple pollen); all of these 18 early bees had large fat bodies in their abdomens (metasomas) that fueled their flights. By March 2, 1992, 5 males in a mating swarm had empty crops and small fat bodies; 7 females collected while flying over the aggregation still had large fat bodies, but they also had filled their crops exclusively with *A. rubrum* pollen, and eggs were developing in their ovaries. The beginning of flowering by *A. rubrum* varies by up to 2 months with weather conditions in early spring; it begins with male flowers and ends about 2–3 weeks later, with female flowers, the trees being usually dioecious and dichogamous. Bloom began on the following dates at Beltsville: April 2, 1978; March 19, 1982; March 6, 1983 (Batra 1985); February 1, 1989; February 12, 1990; February 21, 1991; February 28, 1992; March 24, 1993 and March 13, 1994.

Thermoregulation by Aggregation

Andrena fenningeri is unusual in its use of dense red clay as a nesting substrate, thus resembling *A. macra* (Riddick 1990, 1992). It nested in clay, even though a large area of exposed, sunlit sandy soil was within about 100 m. Most species of *Andrena* nest in more porous, well-drained soils, especially sand (Miliczky and Osgood 1995, Batra 1990); hence they are called "Sandbienen" in German (Gebhardt and Rohr 1987).

On April 21, 1987, when I discovered the aggregation, nests occupied an area of 5 × 8 m. Most nests (53, with tumuli) were in a 3 × 3 m area with exposed soil; it was a buck (deer) scrape, which was renewed every autumn (Fig. 2, site 1). There were 18 nests/m^2, with a minimum internest distance of 1.0 cm. In the part of the aggregation that was in soil covered with short turf (site 2), nests were fewer, spaced up to 1 m apart. On March 8, 1990, the aggregation measured 5 × 34 m; there were up to 54 nests/m^2 in exposed soil (site 1), with internest distances of 4–18 cm ($\bar{x}$ 9.5 cm; N 31). In the turf (site 2), nests were 1–4 m apart. On March 5, 1992, the aggregation measured 2 × 25 m; there were 100 nests/m^2 at site 1 and 30 nests/m^2 at site 2. The aggregation had about 2,900 nests in 1992. By March 1997, the 2 small pine trees near the aggregation had grown, shading it. the bees had moved most nests 2–3 m to the west, where it was sunnier. The winters and early springs of 1997 and 1998 were unusually rainy. Fewer than 100 nests of *A. fenningeri* remained at site 1 by late March, 1998 (1 nest/m^2 maximum density).

Andrena fenningeri nested in the dense aggregation in only one small part of the large field (Fig. 2, Sites 1 and 2). Aggregated nesting by solitary bees and wasps is common, and some aggregations may persist at a site for over 50 years. There are several, nonexclusive explanations for this phenomenon, including substrate limitation; improved efficiency in foraging; protection from predators and parasites; attraction to others of the same species; an opportunity to save time and energy by re-using existing nests; and philopatry, or re-nesting near the insects' natal nests (see review in Rosenheim 1990). Because *A. fenningeri* was active during early spring when the weather was often cold and rainy, the location of its aggregation in the warmest and sunniest part of the field appeared to be most advantageous; this maximized the number of hours available to the bees for foraging and reproduction. Floral resources were abun-

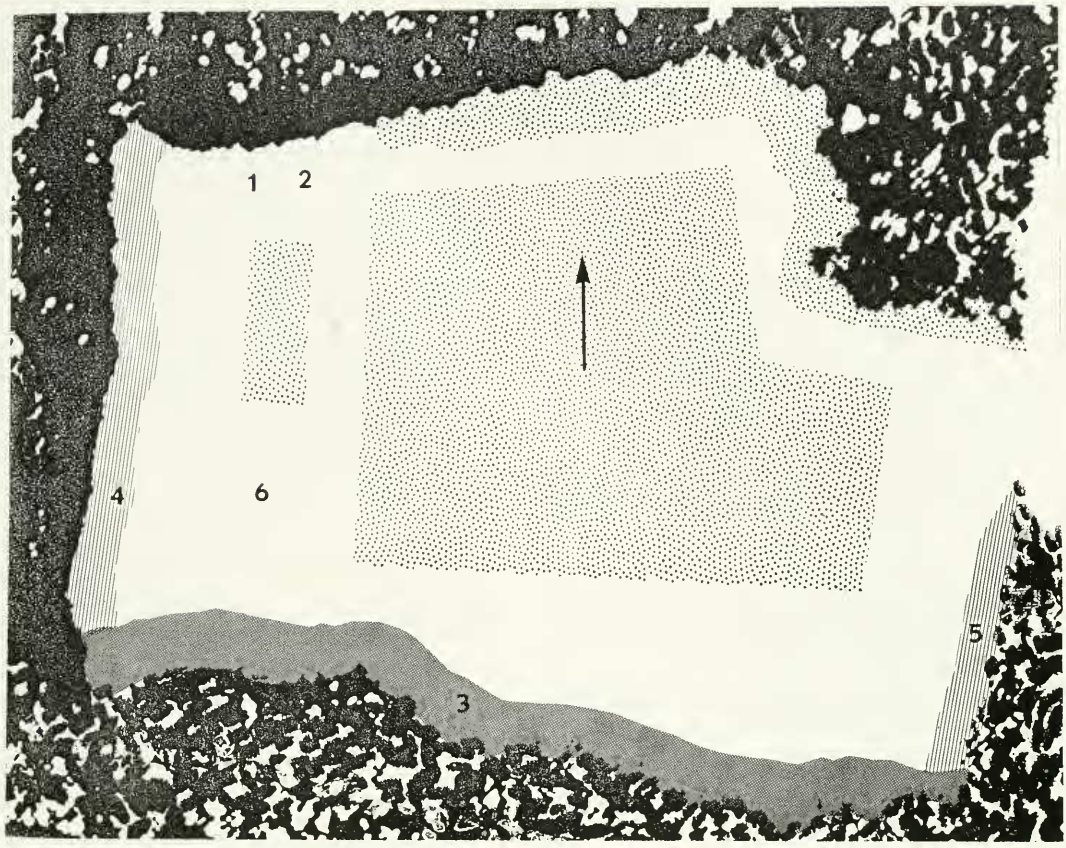

Fig. 2. Field where *A. fenningeri* nested (drawn from aerial photograph). It is 230 m wide, and the arrow points North. Regularly mowed areas of short turf lawn are white (if sunny), striped (if partly shaded) or hatched (if always shaded). Stippled areas indicate locations without nests, being boggy, or fenced and shaded by dense tall grass and shrubs. Temperatures were recorded at locations (Sites) 1–6, all in red marine clay. The main portion of the nest aggregation was in a sunny patch of bare soil at Site 1, and it extended into turf-covered soil (Site 2). There were no nests below the short turf at Sites 3–6; Site 3 was shaded all day; Sites 4 and 5 were shaded in afternoons and mornings respectively; and Site 6 was sunlit all day.

dant, thus not a limitation. The aggregation may have begun decades ago, when a mated founding female successfully nested there, and her descendants returned to the area for nesting (philopatry). Because a closely related, cold-adapted species, *A.* (*Scrapteropsis*) *alleghaniensis,* placed its aggregation of nests in a southeasterly-facing, sandy slope where they received maximum insolation and warmth in early spring (Batra 1990), *A. fenningeri* was suspected of doing likewise, even though its aggregation was in level clay soil rather than in a sandy slope.

In order to test this hypothesis, I made a series of temperature measurements at four depths (2, 8, 15, and 30 cm) at six sites (Sites 1–6, Fig. 2), using bimetallic-dial-probe thermometers. Most of the nest aggregation was at Site 1 (in exposed soil); some nests were in Site 2 (soil covered with short turf).

A split-plot analysis was used on this experiment. The six sites were specifically selected for their shading and vegetation coverage conditions, and are therefore defined as fixed factors in this analysis. The sites are also defined as whole plots of the split-plot design, while the four levels of depth (2, 8, 15, 30 cm) at each site are the sub-

Table 1. Means and Standard Errors for the factorial combination of 4 depths and 6 sites.

Depth	2		8		15		30		
Site	Mean[b]	SEM	Mean[b]	SEM	Mean[b]	SEM	Mean[b]	SEM	Mean[c]
1	11.8	0.77	8.8	0.65	6.7	0.63	5.7	0.56	8.3[c]
2	10.0	0.88	8.7	0.73	8.3	0.71	7.4*	0.62	8.6[c]
3	2.5**	0.82	2.7**	0.68	2.6**	0.66	2.7**	0.59	2.6[c]
4	8.1**	0.89	6.7*	0.73	6.7	0.71	6.1	0.63	6.9[c]
5	8.2**	0.89	6.9*	0.73	6.1	0.71	5.1	0.63	6.6[c]
6	9.9	0.88	7.8	0.73	7.0	0.71	6.7	0.62	7.8[c]
	8.4[d]		6.9[d]		6.2[d]		5.6[d]		

[a] A least-squares-mean test examined possible difference between Site-1 (the one with the greatest nest concentration) means and those of the other five sites. Within a column, a least-squares mean with one asterisk is significantly different from Site 1's mean at $0.01 \leq P \geq 0.05$. A mean with two asterisks is significantly different from Site 1's mean at $P < 0.01$.

[b] Least-square mean.

[c] Mean of all temperature measurements for each site for all four depths.

[d] Mean of all temperature measurements for each depth for all six sites.

plot levels. Measurements of temperature done on different days were defined as haphazard (a random number table was not used). Data were recorded during early afternoon on 7 days from March 3 to March 26, 1992, during the time of peak nesting activity, and used as replication in the analysis. A mixed-model analysis of variance was used to determine the fixed effects of site, depth, and their interaction. A heterogeneous first-order autoregressive covariance structure was included in the ANOVA model to account for the possible associations among depths. Least-significance difference tests ($\partial = 0.05$) were used to compare means of the fixed effects. Results are summarized in Table 1.

Site 1 (the aggregation) was significantly warmer than site 3 at all depths (Table 1). It was warmer than Sites 4 and 5 at depths of 2 and 8 cm, but did not differ from them at 15 and 30 cm. Site 1 did not differ from Sites 2 and 6 at depths of 2, 8 and 15 cm, but, at 30 cm, it was slightly cooler than Site 2, and did not differ from Site 6. The right column of the Table shows the means of all measurements combined from the 4 depths at each site. It shows that the portion of the aggregation at Site 2 was slightly (but not significantly) warmer than the major portion in Site 1, and both of these parts of the aggregation were considerably warmer than areas where the bees did not nest, especially Site 3.

The soil-temperature analysis indicates that *A. fenningeri* used the warmest local area for the aggregation. Thus, the bees thermoregulated by choosing a warm nesting site (and also individually, by basking). Sites 1 and 2 are at the southern edge of a pine-oak forest. The level ground receives maximum insolation at such a location in March (Kimball and Hand 1922, Geiger 1965). The aggregation also benefitted from radiation that was reflected to it from nearby oak tree trunks (see Geiger 1965). Pine trees within the forest broke the cold northwest wind that prevailed on clear, sunny days in Maryland, and they retained heat that was radiated from the soil at night. The protective influence of a forest windbreak to the north of a field edge can raise air temperatures 5 cm above the ground all year, by 11°C above air temperatures in a field near the forest along the opposite, south edge (Wales 1972). Such microclimatic differences are significant; for example, 6 species of vernal wild flowers on a south-facing slope bloomed on average 6 days earlier than the same species growing on a north-facing slope 50 m away; this difference, correlated with cumulative differences in air and soil temperatures, is equivalent to 176 km in latitude (Jackson 1966).

There were slight differences within the aggregation between Sites 1 (exposed soil surface) and 2 (turf covered) that were not statistically significant, but could be detected behaviorally when the temperature in the upper 2 cm of soil was near 11°C (marginal for flight initiation). For example, at noon on March 17, 1992, a sunny day after a frosty night, no bees were flying at either Site 1 or Site 2. At Site 1, temperatures were 11°C at 2 cm, 6.5°C at 8 cm, 4.5°C at 15 cm, and 4.0°C at 30 cm depth. At 15: 30, bees were flying at Site 1 but were not flying at Site 2. At Site 1, soil temperatures by then were 13°C at 2 cm, 10.5°C at 8 cm, 8.0°C at 15 cm and 5.5°C at 30 cm depth. Temperatures then at Site 2 were too cool for flight, being only 10.5°C at 2 cm, 10.0°C at 8 cm, 9.5°C at 15 cm and 6.5°C at 30 cm depth. Although Site 2 was warmer than Site 1 at 15 and 30 cm, it was cooler at 8 cm, and much (2.5°C) cooler at 2 cm depth, where bees usually wait to warm up, before flying. A similar pattern was seen at 13:00 on March 25, 1992, a day of hazy sun after a frosty night: bees were flying at Site 1 but not at Site 2 (Site 1: 14.5°C at 2 cm, 9.0°C at 8 cm, 6.0°C at 15 cm, and 5.5°C at 30 cm depth; Site 2: 11.0°C at 2 cm, 10.5°C at 8 cm, 8.5°C at 15 cm, and 7.5°C at 30 cm). Thus, the sun warmed the upper layers of bare soil at Site 1 more quickly than the same depths in turf-shaded Site 2, permitting flight from Site 1 on cool, sunny days. The insulating turf retained warmth overnight in the lower layers at Site 2, but this did not promote flight activity. Even such slight differences between sites in bare soil and those in turf may be significant for survival among bees that must fly to forage during inclement weather.

Andrena nycthemera also begins adult activity when the soil thaws (as early as February 23 in 1990). Many more bees nested in a sunny part of the aggregation than in a shaded portion, where the soil remained frozen longer, and bees in sunlit areas began seasonal activity several days before those that nested in shady portions of the aggregation areas (Schönitzer and Klinksik 1990). Slight microclimatic differences also influence the nesting behvior of halictine bees (Batra 1997, Potts and Willmer 1997).

Thermoregulation by Individuals

Species of *Andrena* that were investigated by Stone and Willmer (1989) produce relatively little endothermic heat, compared to some other genera of bees; instead they depend on insolation and warmth from substrates to generate the minimum 8–12°C ambient temperature needed to begin flight. Many species of *Andrena* bask at nest entrances and on vegetation before takeoff on sunny, cool days. They include *A. fulva* Müller (Paxton 1991), *A. erigeniae* Robt., which basks on fallen leaves that are 6–9°C warmer than ambient temperatures (Barrows 1978), and *A. nycthemera,* which can begin flights after basking at 8–10°C on sunny days, but cannot fly on cloudy days until the ambient temperature reaches 15°C (Schönitzer and Klinksik 1990). Herrera (1995) found that *A. bicolor* F. foraged on sunny days with an air temperature of at least 12–13°C; these small bees bask in warm microclimates to achieve the minimum internal thoracic temperature of 22°C needed to begin flight.

Both sexes of *A. fenningeri* were able to begin flight on sunny days when the ambient temperature of their microclimate was at least 11°C. Bees were often seen basking just inside nest entrances, on tumuli, beneath or on fallen leaves, and on vegetation. The nearly black bodies of both sexes of *A. fenningeri* bear pale hairs, which are densest over the thorax (where warm-up of flight muscles is needed). In this way, the bees resemble the "heat-trap" structures of pussy willow flowers, which have been shown by Krog (1955) to absorb shortwave light (solar radiation), which passes through pale hairs into their black surfaces, and there becomes long wave radiation (heat), which is trapped in the dead airspace among the pale hairs.

Although *A. fenningeri* required a minimum, insolated temperature of 11°C to begin flying, they were active inside their nests at much lower temperatures. On January 11, 1990, the soil at the aggregation (Site 1) had thawed after an unusually cold December 1989 (−20°C air temperature for several days, freezing the soil). I excavated twenty-seven cells on January 11, to study the phenology of the bees and determine how they can emerge so early each spring. The air temperature (at 1 m, in shade) was 10°C, and soil temperatures were 6°C at 2 cm, and 4°C at 10, 21 and 30 cm depths. Some bees had already emerged from their cells (4 ♂ and 3 ♀); 9 males and 11 females were still in their cells (sex ratio near 1:1). Those in cells were resting on their backs. Bees that had emerged stood upright and had dug as far as 2 cm toward the surface; the earth that they had excavated was pushed backward, and packed into their natal brood cells, covering the fecal layer that had been deposited before their transformation to prepupae late the previous May. When these cold (4°C) bees were disturbed, they vibrated their wings; when they were warmed slightly, they stood upright and began to walk. These bees were stored in tissue culture wells at 4°C for 4 days. Some of them defecated (pale meconium), others chewed on moist soil that was placed in the wells with them. Thus, they were active at low temperatures.

At the aggregation, air temperatures were above normal for January 1990, and by the 18th, the air temperature at 14:00 E.S.T. (1 m, shade) was 16°C, and soil temperatures were 13°C at 2 cm, 12°C at 10 cm (both above flight threshold), 10°C at 21 cm, and 8°C at 30 cm. During January, the bees worked their way toward the surface, and the first bees (males) were flying on February 9, a sunny day, when the air temperature at 14:00 (at 1 m, in shade) was 17°C, and soil temperatures at Site 1 were 11.5°C at 2 cm, 10°C at 10 cm, 8.5°C at 21 cm and 7.5°C at 30 cm. *Acer rubrum, Draba* and *Salix* had just begun to bloom (Fig. 3).

These early males flew slowly, about 2–7 cm above the aggregation (Site 1 only), frequently stopping to bask on dead oak leaves on the ground. Flying males dropped to the ground when clouds obscured the sun and when disturbed by the observer; they could then be captured by hand. On February 12, more nests were examined. One female had partly emerged from her cell at a depth of 17 cm, 3 others had emerged, and were in the soil at depths of 3, 9, and 11 cm, having moved toward the surface. No males remained in their cells; 2 were found in the soil at 3 and 6 cm depths. Soil temperatures were 11°C at 2 cm, 8°C at 20 cm and 6°C at 20 and 30 cm. Only males were seen again the next afternoon (sunny, 15°C), circling low over the aggregation in calm air, but they settled on the ground and crawled around when gusts of wind or clouds arrived. The males made intermittent circular flights over small areas (20–30 cm radius), which gradually moved across the aggregation. No territoriality or male aggression was seen, and the males were not seen in nearby trees, where they formed mating swarms later in February. Female *A. fenningeri* released a pungent citrus odor from their mandibular glands when handled, but males had little odor. Possibly the patrolling males can smell the mandibular gland pheromone, released as the females dig their way toward the surface.

On February 28, 1991, male behavior was similar. Fresh tumuli indicated that some females had begun nesting, but none were flying. Many males were patrolling near the ground in a zigzag pattern, often entering and leaving nests. When shaded, they dropped to the ground, and could be picked up by hand; they could not fly even though they buzzed vigorously, an activity that should warm their flight muscles. They were able to resume flight when replaced in the sun for about a minute. These small males could warm up in the sun at marginal temperatures more quickly than could the larger females, which may explain the absence of flying females. The air temperature

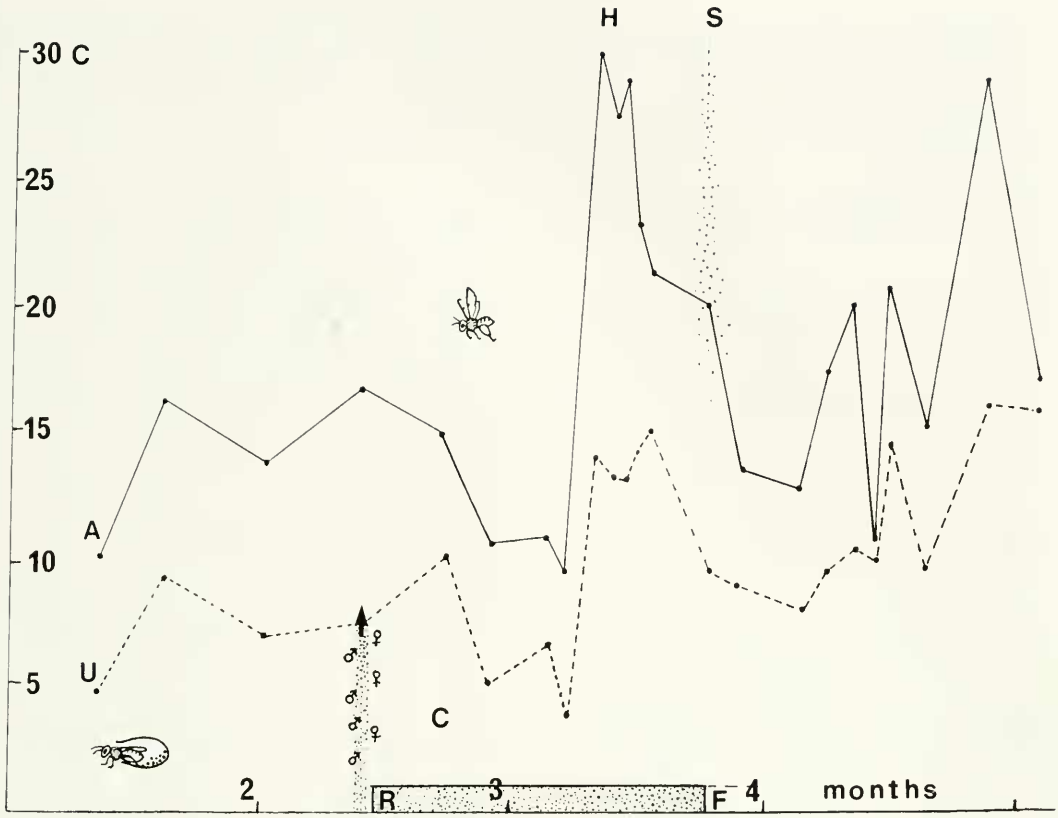

Fig. 3. Temperatures at the nest aggregation (Site 1) and phenology of *A. fenningeri* from January 11 through May 1, 1990, a warmer than normal spring. A, air temperatures at 1 m height in shade; U, underground soil temperatures at a depth of 30 cm. Bees began emerging from brood cells in January; then crawled up the tunnels of their natal nests in early February. Red maples (R bar) bloomed from February 9 to March 21. The first bees (males) emerged February 9; female bees began collecting pollen from red maple by February 22; when maples finished blooming, bee activity declined and females switched to other pollen sources, including fruit trees (F). By May 4, the forest canopy had leafed out, the clay soil at the aggregation had dried and hardened, and only a few senile bees remained. From March 6–15, a record heat wave, with southwest winds, prevailed (H), and the bees were unusually active; on March 16, a cold front brought rain, and snow (S) fell on March 20 and on March 24–25.

(14:30, in shade at 1 m) was 13.5–14.0°C; the soil (Site 1) at 2 cm was 10°C; at 20 cm, 7.5°C and at 30 cm, 7°C. Males that had dropped to the ground to avoid wind often crawled beneath sunlit, dead, dry oak leaves, where temperatures were 12–15°C. In early March, in bright sun, temperatures under sunlit oak leaves reached 22°C when the ambient air temperature was 18°C. In early March 1992, some males that had been flying among trees in the mating swarm basked in the sun on dead leaves, but they crawled under the leaves when the wind gusted or clouds passed; some slept overnight in nest tunnels. When the air temperature at 1 m (shade) on a hazy day was at the 11°C threshold for flight, no female bees flew, but males were able to fly slowly for short distances between bouts of basking in the weak sunlight. On a cloudy day, with air at 11°C, the temperature was only 10°C below a fallen leaf, and also at 2 cm in the soil; insolation was insufficient on cloudy days, thus, no bees flew.

Because *A. fenningeri* made more nests in the portion of the aggregation that was

in bare soil (Site 1) than in the part that was in short (2–4 cm) turf (Site 2), and because bees emerged earlier each spring at Site 1 than at Site 2, soil temperatures at Site 1 were compared with those at Site 2. Although no statistically significant temperature difference between Sites 1 and 2 was detected in March, 1992 (see Table 1), there were small differences between the sites that may have been sufficient to account for the slightly earlier, and slightly more, activity at Site 1, especially early in the spring, when temperatures marginally permitted flight.

Temperatures were measured at Sites 1 and 2 at the same time of day (early afternoon) on 13 days in March and April, 1990 and 1993. Site 2 was cooler than Site 1 by a mean of 2.6°C at 2 cm, and by 1.1°C at 8 cm; Site 2 was warmer than Site 1 by 0.4°C at 15 cm and by 1.4°C at 30 cm depth. Evidently, the upper levels of bare soil (Site 1) warm more rapidly each sunny day than the same levels under grass, but the insulating grass (Site 2) retains warmth at lower levels overnight. The difference between Sites 1 and 2 was most prominent during sunny weather, for example on March 8, 1990, a sunny day after a clear, cold night, at 2 cm depth (where bees wait before flights), Site 1 was 14°C (warm enough for bees to fly), but Site 2 at 2 cm depth was only 10°C, which was below the flight threshold. However, after a several days of rain on a cloudy day, there was little difference between Sites 1 and 2.

The behavior of male *A. fenningeri* in mating swarms was also influenced by microclimate. At first, males flew only a few centimeters above the warm ground, where most nests were aggregated. As the air temperature warmed, many males moved their patrolling to the tips of the branches of small (4–5-m-tall) pine trees near the aggregation, where they formed swarms. On February 28, 1992, males swarmed around the pine trees at an air temperature (1 m, shade) of 17.5°C. When clouds or haze arrived, the males suddenly ceased flying, alighted, and crawled between the dark green pine needles (which would retain heat); they resumed their flights when the sun reappeared.

Behavior of Males

The behavior of male *Andrena* bees has been described and reviewed by Barrows (1978), Gebbardt and Röhr (1987), and Hallmen (1991). Males may emerge simultaneously with, or earlier than, their females each year. They swarm conspicuously in the sunshine, circling and zigzagging above aggregations of nests, around flowers of host plants, and around tall landmarks, such as selected trees near aggregations. Males of most species are non-territorial, and they jointly patrol in search of females, without noticeable interactions among males. Males of *A. nycthemera* are unusually aggressive, biting each other and competitively digging in the ground, searching for emerging females (Shönitzer and Klinksik 1990). Despite the large numbers of both sexes that emerge and mate within a few days, and the numerous times males are seen pouncing on females and on various small dark objects, actual copulation is surprisingly rarely observed. I also did not observe the mating of *A. fenningeri,* in spite of many hours spent watching their behavior.

Both sexes of *A. fenningeri* produce a lemon-like odor from their mandibular glands when captured. It is most distinct in females. The mandibular gland secretions of some *Andrena* bees contain complex mixtures of spiroacetals, monoterpenes, and other compounds (Bergström and Tengö 1982). The secretion of *A. fenningeri* probably includes geraniol and citronellol, which are major components in other species of *Andrena* (Bergström and Tengö 1982). Male bees use these secretions to mark the areas that they patrol in search of females (Bergström and Tengö 1982, Gebhardt and Röhr 1987, Hallmen 1991); and female bees use both mandibular-gland and Dufour's-gland secretions to mark and iden-

tify their nests (Ayasse et al. 1990; Steinmann 1990).

During an unusually warm spring, the first male *A. fenningeri* emerged on February 9, 1990, before the females. They emerged as late as March 7, in 1993, also before the females appeared. Some years, males flew before any host plants bloomed; in other years, the first bees appeared when hosts started blooming. *Andrena nycthemera* males also may begin flying before any food is available (Schönitzer and Klinksik 1990). During their first activity, males crawled, or patrolled, flying in the sunshine some 2–8 cm above the bare soil at Site 1, which radiated heat, warming the relatively calm layer of air near the ground. They flew upwind in small circles or in slow, wavering patterns, occasionally waiting on fallen leaves when clouds passed. They also fell to the ground and "froze" when alarmed (by my movements) and could be caught with the fingers. On cool days, newly emerged females also displayed such thanatosis, when disturbed, becoming immobile, dropping to the ground, with legs held stiffly, parallel and close to their bodies, a behavior similar to that of elaterid beetles. Sometimes, such bees relaxed, and slowly crawled beneath dead leaves. This behavior was seen only in early spring, before host plants began to bloom. Perhaps it is an energy-conserving defense mechanism, used at a time when the bees were subsisting on their stores of fat. Male *A. fenningeri* were seen entering and leaving exit holes and nest entrances. Some males slept in holes, but they did not dig for females. Occasionally, both males and females crawled on the surface of the aggregation, but mating was not seen there.

Most females emerged each year after one or more warm, sunny days, and fresh tumuli indicated that nesting had begun. At this time, many male *A. fenningeri* ceased patrolling at the aggregation, and instead, they swarmed among the bare branches of an oak tree and around two small pines (*P. virginiana* Mill.) growing next to the aggregation. Males of both *Nomada sayi* Robt. and *N. perplexa* Cress. swarmed together with the males of *A. fenningeri*, both at the aggregation and around the trees; perhaps they have similar pheromones. Male *A. fenningeri* were seen to emerge from the ground and fly up to join these others around the trees.

Males of *A. fenningeri* patrolled areas around the tips of the pine branches. They zigzagged along the downwind sides of the branches at a height of 2–4 m, occasionally alighting. They flew from one branch tip to the next, briefly hovering while facing the tip of each branch, before flying upwind to the next branch, where they zigzagged toward its tip. This was repeated, until they reached the upwind (and sunny) side of the tree, from which they drifted back on the breeze, to repeat the process of inspecting branch tips. Mating was not observed at these "swarm trees." Similar upwind and zigzag patrolling, alternating with downwind drifting, occurs in *A. vaga* (Hallmen 1991).

On March 2, 1992, an attempt to attract males to females in a swarm was made. Four live females were tied with threads to the tips of pine branches where many males patrolled. They were conspicuous, but were bypassed by 16 males. Another 7 males hovered to briefly inspect them, and 4 males pounced on the females, but immediately released without mating. These females orally released a distinct lemon-like odor. Other bees that were swarming around the pine trees were netted, yielding 10 males and 1 female, indicating that females were also attracted to these "swarm trees" (see Hallmen 1991). The captured female and 5 males were dissected; the female was inseminated and had fed on maple pollen, but the males had not eaten pollen or nectar, their crops being collapsed and their guts empty. A sample of 6 females that were flying over the aggregation on March 2 had all eaten maple pollen, and all were inseminated. Similarly, on February 28, 1992, 14 males that were swarming

around the pine trees were dissected; 12 had empty crops and guts, 1 had eaten nectar, 1 had eaten some maple pollen; and most had large fat bodies. The females that were collected from nests with tumuli on that day varied: 1 had not mated or eaten, and still had rectal meconium; 2 were inseminated but had not eaten. The number of males seen around the swarm trees and above the aggregation each year slowly declined as spring advanced, and a week to 10 days after emergence, males were no longer seen near the aggregation. By this time, host plants were blooming, and the males searched for females there.

Parasites and Associates

As with other species of *Andrena* worldwide, *A. fenningeri* was associated with several other insects at the aggregation. These included the halictine bee, *Dialictus versatus* (Robertson), nesting at the western edge of the aggregation, and its cleptoparasite, *Sphecodes stygius* Robertson. Five species of *Nomada* were active at the *A. fenningeri* aggregation, which I identified as *N. bella* Cresson, *N. cressoni* Robertson, *N. parva* Robertson, *N. perplexa* Cresson and *N. sayi* Robertson. *Nomada perplexa* was by far the most abundant of these cleptoparasitic anthophorid bees. They often entered nests, but I did not find any *Nomada* in brood cells. A conopid fly (probably *Myopa* sp.), bombyliid flies, blue and black fungi in brood cells, and three species in the genus *Eustalomyia* (Anthomyiidae) also were present. These anthomyiids were attracted to flying *A. fenningeri,* but not to *D. versatus,* which had a different, more erratic flight pattern.

The grouping of nests in a perennial aggregation permitted a permanent population of these natural enemies, but the bees had several defenses against them. For example, many nests were initiated beneath dead leaves, which concealed their entrances; tumuli often were not rebuilt when they had been destroyed by rain, which made nest entrances inconspicuous; nest entrances were temporarily sealed with soil particles; returning foragers dodged cleptoparasites that followed them; foragers took circuitous routes, and entered nests abruptly, thus confusing and evading trailing parasitic bees and flies. Such evasive techniques have been seen in other species of solitary bees and wasps (Hager and Kurczewski 1985, Meyer-Holzapfel 1986, Rosenheim 1990, Schönitzer and Klinksik 1990).

The most abundant of all the parasites were three *Eustalomyia* species (det. W. Downes, Jr.). The only hosts previously known for this genus of anthomyiid flies are the solitary crabronine wasps, *Ectemnius paucimaculatus* (Packard) in North America (Krombein 1964), and *E. cavifrons* (Thomson) in Europe (Meyer-Holzapfel 1986). According to Downes (in litt.), the three species that are associated with *A. fenningeri* may be the first to be associated with bees, and probably are new records, because these flies appeared much earlier in spring than those species that are associated with crabronine wasps.

The *Eustalomyia* species appeared in succession; of samples sent for identification, the first (species A, males) being active at the aggregation as early as March 9, 1992, 12 days after the first bees emerged that year. Females of species A were active at the aggregation March 15–22, 1990, and March 25, 1988; species-A males were found as late as April 27, 1988. Females of species B were collected at the aggregation on April 4, 1988, and females of species C were present on April, 27, 1988.

The behavior and gross morphology of all three species of *Eustalomyia* were similar. It was not possible to distinguish among them in the field; thus, they will be discussed collectively here. Initially, they were assumed to be the anthomyiids, *Leucophora obtusa* (Zetterstedt), and *L. marylandica* (Malloch), which are common at aggregations of three species of *Colletes* bees at Beltsville, and behave similarly to *Eustalomyia. Leucophora obtusa* also par-

asitizes *Andrena nycthemera* in Europe (Schönitzer and Klinksik 1990).

Cleptoparasitic anthomyiid and sarcophagid flies are often classified according to their behavior in relation to their hosts. Some are "satellite flies," also called "station takers," which perch near the nests of hosts, abruptly taking flight to pursue returning foragers to their nests. Others are "hole searchers," flying about in search of hosts' nests (Hager and Kurczewski 1985, Wcislo 1986, Meyer-Holzapfel 1986). The host bees and wasps defend their nests against satellite flies by evasive maneuvers in flight. Intense activity by both hosts and parasites at dense aggregations also causes confusion of the parasites. Closure and concealment of nest entrances provide some protection from hole-searching flies and the cleptoparasitic bees, *Nomada* and *Sphecodes* (see review in Rosenheim 1990).

A 1-m^2 area in the densest part of the aggregation (54 nests/m^2 on March 8) was watched for 74 minutes on a warm, sunny day (10:10–11:24, March 15, 1990), in order to observe the activities of cleptoparasites, especially *Eustalomyia*. During this time, *A. fenningeri* foragers left nests 4 times and returned with yellow pollen 10 times (one trip lasted 14 minutes); two bees remained at nest entrances; usually, one *Nomada parva* continually patrolled above the nests; once one alighted briefly, to fan her wings at a nest entrance (probably to bring up odors from the nest).

Most of the time, two *Eustalomyia* were perched in the area. The flies jumped up and briefly followed patrolling *Nomada* twice; they chased each other once; and one briefly followed a falling leaflet. One or two flies 10 times followed *A. fenningeri,* while both leaving and returning to their nests. Flies were seen entering *A. fenningeri* nests 3 times. In one instance, two flies followed a bee returning with pollen; one of them alighted and peered into the nest headfirst, then turned and slowly backed into the nest, until it disappeared. After 4 minutes, it reappeared at the entrance, waited 10 seconds, and flew away (the bee remained inside). Another time, two flies followed a bee returning with pollen (she zigzagged in an attempt to lose them); one fly followed this bee into her nest headfirst, but left within a minute. Once, two flies followed a bee laden with pollen to her nest entrance, which was beneath a fallen leaf. On alighting near the nest, the flies shoved each other for 1–2 seconds, until one of them flew away. The "winner" then slowly backed tailfirst into the nest entrance, rested there for 2 minutes, then backed down into the tunnel, out of sight. After another 4 minutes, the fly's head reappeared at the entrance, the fly walked out of the nest and rested for 2 minutes facing away from it, cleaned itself, and departed.

The bees defended their nests in several ways. The entrances to many nests were closed with plugs of soil or obscured by loose tumuli. Entrances to other nests were camouflaged by, or hidden beneath, dead leaves, grass blades, and twigs. Bees that appeared to be ready to leave their nest entrances on foraging trips were hesitant, backing down when other insects flew nearby; departing bees were briefly followed by flies, but they did not seem to take evasive paths. Ten bees, returning to their nests that were followed by *Eustalomyia,* performed elaborate evasive maneuvers before abruptly diving into their nests' entrances. In contrast, two returning bees that were not followed by flies entered their nests directly. During evasive flights, returning bees pursued by flies zigzagged; one of them left the area for 2 minutes, returning to her nest again without the fly; another bee shook off two closely-following flies when she crawled beneath a leaf to the hidden entrance of her nest; a third bee had nested in the shadow of a large piece of debris; the pursuing fly did not follow her, but alighted in a sunny area nearby. Another bee had nested in turf; this bee hit the grass blades and fell to the ground when she tried to zigzag to evade two pursuing flies. The placement of nests in shadows beneath de-

bris may help prevent *Eustalomyia* attacks, but this may also be disadvantageous because less warmth (insolation) would be present at such shady sites.

Adult *Eustalomyia* spp. first appeared at the aggregation soon after the bees began to emerge. *Nomada perplexa* emerged at the same time as their hosts, and even shared mating aggregation sites with *A. fenningeri*. On cool, sunny days in early spring, *Eustalomyia, Nomada,* and their hosts basked on the warm soil at the aggregation. The initiation of adult activity by these insects in February through March varied by up to a month in different years, but the time of its termination each year in early May varied by only about a week.

Only one small maggot was found (May 4, 1989), although 22 nests of *A. fenningeri* were examined, and *Eustalomyia* were abundant. It was on the side wall of a sealed cell that contained a normal egg on an intact pollen ball, in a marked nest. This nest was closed at the surface, with only this one cell, at the end of a backfilled lateral. This cell was being provisioned on April 21, and *Eustalomyia* had been very active at the aggregation. At that time, this nest had a tumulus; probably it was a new, secondary nest. There was no bee in this closed nest when it was examined on May 4. The genus *Eustalomyia* is ovoviviparous (Meyer-Holzapfel 1986). Those species associated with crabronine wasps oviposit at the host's nest entrances; the fly larvae hatch immediately, and crawl to the wasps' food stores (Meyer-Holzapfel 1986). In contrast, the species that are associated with *A. fenningeri* enter the bee's nests, even while the adult bee is still inside, and they somehow manage to deposit their eggs (or perhaps larvae) inside cells that have been completed, but not yet sealed (the cell plug and long, backfilled lateral would probably prevent these delicate flies and their maggots from entering sealed cells). Because solitary bees immediately begin to seal their brood cells and backfill laterals on completing oviposition, which occurs after a period spent smoothing and perfecting the pollen ball (Batra 1970), it would be difficult for the flies to seize this opportunity. If flies oviposited in cells before pollen balls are completed, the gyrations and grooming of the pollen ball by the bees working in the confinement of their cells would damage fly eggs or larvae, and if detected, the bees may kill, eat, or remove them. On March 22, 1990, one *Eustalomyia* fly that had backed into a nest that was occupied by a bee, as if to oviposit, rapidly emerged while buzzing its wings, agitated, as if it had been attacked by the defensive bee. It then waited, 1 mm from the nest entrance and facing it, for the next 33 minutes. Perhaps the flies deposit their eggs in crevices in open laterals and the hatchling larvae slip into the open cells while the bees are temporarily quiescent, during the process of oviposition.

Conopid flies also parasitize these bees. On May 7, 1987, two dead female *A. fenningeri* were found, one in each of two nests. In both instances, the bee, with swollen abdomen, was poised over a completed pollen ball, as if to begin oviposition (Fig. 1D). One of them contained a brown puparium; a large maggot emerged from the pulsating abdomen of the other bee 30 minutes after her collection. Evidently, the pressure of the maggots inside the bees mimicked the stimulus of eggs that were ready to lay, causing the bees to prepare normal-appearing pollen balls, and take the position for egg laying, as they died (there may have been additional stimuli). Both nests had other cells with eggs on pollen balls, suggesting that these bees had laid eggs soon before the rapidly-growing maggots consumed most of their abdominal contents. According to Smith (1966), *Andrena* bees are usually parasitized by species of conopid flies in the genus *Myopa*; host bees may actively fly and feed with a large maggot nearly filling the abdomen; death of the bee occurs shortly before the maggot's pupation.

Conclusion

Andrena fenningeri is a species of solitary, vernal, univoltine bee that successfully exploits ecological resources that become available as soon as the ground thaws. In order to be prepared for the earliest bloom, this bee nests in permanent aggregations in the warmest available microhabitat. Overwintered adults begin to move out of their natal brood cells toward the surface in midwinter. On emergence from nests, they mate, often before food is available, and soon females begin to excavate new nests in the aggregation. When the temperature is marginal for flight, these black bees bask in the sun, to gain sufficient warmth for their activities.

This species first feeds on early-blooming red maple and willow, but later shifts to pear and peach as they begin to bloom. It may be possible to manage this species for orchard pollination, if suitable nesting sites and early-season hosts are provided. Areas of sunny, exposed, level clay soil along the north edges of orchards could be prepared and kept free of vegetation. They should be backed along their north sides by windbreaks, such as forests, walls, or solid fences. Red maples and willows should grow within 100 m. The initial population of bees could be obtained by transplanting cores of soil that contain nests from an existing aggregation, as is done to move soil-dwelling alkali bees (Batra 1970). Once a population of bees is established near the orchard, it would become permanent and maintenance-free, except for the need to remove (scrape) all vegetation from it each winter to permit maximum insolation in early spring.

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